

Movements of Fluvial Bonneville Cutthroat Trout in the Thomas Fork of the Bear River, Idaho–Wyoming

WARREN T. COLYER*

Trout Unlimited, 249 South 100th West, Providence, Utah 84332, USA

JEFFREY L. KERSHNER

Fish and Aquatic Ecology Unit, U.S. Forest Service,
Aquatic, Watershed, and Earth Resources Department, Utah State University,
5210 University Hill, Logan, Utah 84322-5210, USA

ROBERT H. HILDERBRAND

University of Maryland, Center for Environmental Science, Appalachian Laboratory,
301 Braddock Road, Frostburg, Maryland 21532, USA

Abstract.—The majority of interior subspecies of cutthroat trout *Oncorhynchus clarkii* have been extirpated from large rivers by anthropogenic activities that have fragmented habitats and introduced nonnative competitors. Selective pressures against migratory behaviors and main-stem river occupation, coupled with conservation strategies that isolate genetically pure populations above barriers, have restricted gene flow and prevented expression of the fluvial life history in many populations. Existing knowledge about the movements and home range requirements of fluvial cutthroat trout is, therefore, limited. Our objectives in this study were to (1) determine the extent of seasonal home ranges and mobility of Bonneville cutthroat trout *O. c. utah* (BCT) in the Thomas Fork and main-stem Bear River and (2) evaluate the role of a water diversion structure functioning as a seasonal migration barrier to fish movement. We implanted 55 BCT in the Thomas Fork of the Bear River, Idaho, with radio transmitters and located them bimonthly in 1999–2000 and weekly in 2000–2001. We found fish to be more mobile than previously reported. Individuals above the diversion barrier occupied substantially larger home ranges than those below the barrier (analysis of variance: $P = 0.0003$; median = 2,225 m above barrier; median = 500 m below barrier) throughout our study, and they moved more frequently (mean, 0.89 movements/contact; range, 0.57–1.00) from October 2000 through March 2001 than fish below the barrier (mean, 0.45 movements/contact; range, 0.00–1.00). During the spring of both years, we located radio-tagged fish in both upstream and neighboring tributaries as far as 86 km away from our study site. Our results document the existence of a fluvial component of BCT in the Bear River and its tributaries and suggest that successful efforts at conservation of these fish must focus on main-stem habitats and the maintenance of seasonal migration corridors.

Interior subspecies of cutthroat trout *Oncorhynchus clarkii* have suffered precipitous declines during the last century. Anthropogenic activities have fragmented habitats (Thurow et al. 1988; Rieman and McIntyre 1993) and impeded migrations, causing reductions in fluvial populations and the extirpation of cutthroat trout subspecies from most main-stem river habitats (Gresswell 1988, and references therein; Behnke 1992; Young 1995). The majority of extant cutthroat trout populations now comprise resident, nonmigratory individuals in headwater tributary systems (Young 1995). Such isolated populations may face shorter times to ex-

inction because of insufficient habitat (Dunning et al. 1992; Hilderbrand and Kershner 2000a; Harig and Fausch 2002) and demographic and environmental variability (Gilpin and Soule 1986; Rieman and Allendorf 2001; Hilderbrand 2003)—risks that could be mitigated with minimal amounts of immigration (Stacey and Taper 1992; Hilderbrand 2003). Contemporary salmonid populations with access to large main-stem systems often have important fluvial components (Swanberg 1997; Schmetterling 2001, 2003), and we can infer that many historical cutthroat trout populations probably shared this characteristic.

Recent efforts to conserve interior subspecies of cutthroat trout have usually entailed the isolation of genetically pure populations above impassable barriers (Stuber et al. 1988; Moyle and Sato 1991; Young 1995; Novinger and Rahel 2003). While

* Corresponding author: wcolyer@tu.org

Received May 18, 2004; accepted January 31, 2005
Published online July 20, 2005

potentially effective in forestalling genetic introgression or displacement by nonnative fishes, this "conservation by isolation" approach selects against mobile individuals and may cause extirpations of local populations (Morita and Yamamoto 2002). Genetic selection against migrants can be very strong above barriers (Northcote 1992), and major meristic, genotypic, and behavioral differences between individuals above and below barriers have been documented (Northcote et al. 1970; Young 1996; Morita et al. 2000). The efficacy of isolation as a conservation tool has now been challenged by research suggesting that space and habitat availability may be insufficient to ensure species' persistence in many headwater systems currently occupied by remnant and translocated cutthroat trout populations (Hilderbrand and Kershner 2000a; Young and Harig 2001; Harig and Fausch 2002).

Criticisms of the spatial scales at which conservation schemes have historically been approached are supported by research suggesting that stream salmonids can be highly mobile. In large river systems where connectivity remains intact, individuals often move substantial distances in association with spawning migrations and relocations to seasonal habitats (Bjornn and Mallet 1964; Clapp et al. 1990; West 1992; Young 1994; Brown and Mackay 1995; Jakober et al. 1998; Schmetterling 2001). The fluvial life history strategy is typified by a spawning migration from a main-stem river into a tributary (Behnke 1992) and contrasts with the resident, nonmigratory strategy exhibited by individuals in isolated systems. Studies suggest that salmonid populations can comprise both resident and fluvial life history strategies (Rieman and McIntyre 1995; Henderson 1999). Within the few interior cutthroat trout populations that still inhabit connected large river systems with suitable habitats, fluvial life histories persist (Liknes and Graham 1988; Schmetterling 2001); however, for the majority of interior subspecies of cutthroat trout, connectivity between populations has been lost and the migratory life history strategy is no longer expressed (Young 1995).

Studies of fluvial cutthroat trout movements have been rare (but see Bjornn and Mallet 1964; Henderson et al. 2000; Schmetterling 2001); we know of only one study of fluvial Bonneville cutthroat trout *O. c. utah* (BCT) in a medium-sized river (Bernard and Israelsen 1982). Current knowledge about the movement patterns and home ranges of fluvial cutthroat trout (and BCT in particular) is, therefore, limited and largely confined to move-

ments within a single season. The few studies that have addressed winter movements of cutthroat trout have found individuals to be sedentary during this season (Brown and Mackay 1995; Jakober et al. 1998; Brown 1999; Hilderbrand and Kershner 2000b; Schmetterling 2001), although westslope cutthroat trout *O. c. lewisi* in Canada did move in response to frazil and anchor ice formation. Limited winter movements have also been documented for other salmonid species (Chisholm and Hubert 1987; Swanberg 1997; Jakober et al. 1998) and have been attributed to metabolic decreases associated with lower water temperatures and the resulting need to conserve energy (Cunjak and Power 1986).

The Thomas Fork of the Bear River in southeastern Idaho affords a rare opportunity to study fluvial BCT in a large river system. Connection between the Thomas Fork and main-stem Bear River is maintained throughout much of the year, but is seasonally disrupted by irrigation diversions and water quality limitations. Large (>400 mm) BCT are found in both the Thomas Fork and the Bear River and appear to seasonally move within and between the two rivers. We used radiotelemetry to monitor movements of BCT initially tagged in the Thomas Fork of the Bear River during 1999–2001. Our objectives were to (1) determine the extent of seasonal home ranges and mobility of BCT in the Thomas Fork and Bear River to gain a better understanding of spatial requirements, and (2) evaluate the role of a water diversion structure as a seasonal migration barrier to fish movements.

Study Site

The Thomas Fork is a fourth-order tributary to the Bear River and drains a 584-km² watershed in southeastern Idaho and western Wyoming. Our study site was located within a 4-km² section of the Bear Lake National Wildlife Refuge located at the lower end of the Thomas Fork valley just upstream from its confluence with the Bear River (Figure 1). The Thomas Fork is low gradient and highly sinuous and has an average bankfull width of 10 m within the study area. Riparian communities are dominated by willows, grasses, and sedges. The predominant substrate is silt, and macrophytes blanket the water surface throughout much of the summer and fall. Mean annual discharge ranges from 0.3 to 8.5 m³/s; annual peak flow varies by an order of magnitude (2.8–28.3 m³/s). The annual range of water temperatures is large (0–25°C), and summer temperatures can exceed the laboratory-derived upper incipient lethal tem-

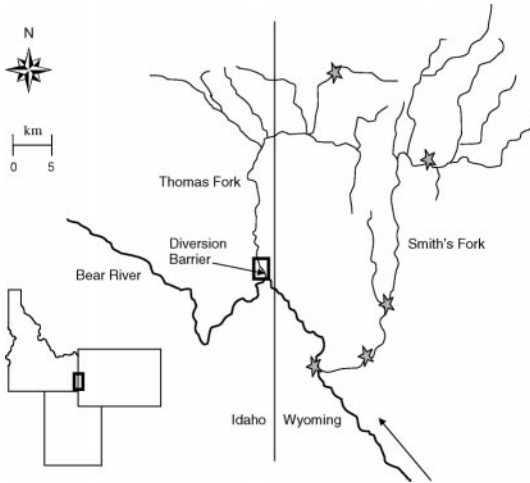


FIGURE 1.—Map of Thomas Fork and Bear River study site and surrounding area, Idaho–Wyoming. Stars represent last locations for five Bonneville cutthroat trout that were successfully tracked through spring migrations in 2000 and 2001. All fish were initially captured and released in the study section outlined by the rectangle on Thomas Fork.

perature for BCT (24.2°C; Johnstone and Rahel 2003; Schrank et al. 2003).

A small diversion structure spans the Thomas Fork 2 km upstream from its confluence with the Bear River. Water passes through this structure via two adjacent culverts and a 1.5-m-high spillover. A concrete splash pad at the spillover prevents fish from leaping upstream, so the structure allows upstream fish passage only when the culverts are not blocked for irrigation purposes (usually late fall through winter).

Bonneville cutthroat trout is the only native salmonid that inhabits the Thomas Fork and Bear River, although nonnative rainbow trout *O. mykiss* and brown trout *Salmo trutta* are present elsewhere in the drainage. To date, researchers have found no evidence of genetic introgression between Thomas Fork BCT and rainbow trout (Martin and Shiozawa 1982; Behnke 1992; Shiozawa and Evans 1995). Bonneville cutthroat trout were petitioned for listing under the Endangered Species Act in 1998 and are currently designated as a “sensitive species” by the U.S. Forest Service and Wyoming and a “species of concern” in Utah and Idaho (Kershner 1995).

Methods

Using a boat-mounted electrofishing unit (Cof-felt Manufacturing, Flagstaff, Arizona, VVP unit),

we electrofished sections of the Thomas Fork above and below the diversion structure during October 1999 and 2000. All BCT were anesthetized with tricaine methanesulfonate (Finquel brand; 70 mg/L), weighed to the nearest gram, and measured to the nearest millimeter (total length). During 1999 and 2000, we implanted 55 fish with radio transmitters (Advanced Telemetry Systems, Asanti, Minnesota, Model 357) following techniques described by Bidgood (1980) and Schill et al. (1994). We limited transmitter weight to less than 2% of body weight as suggested by Winter (1996). After surgery, fish were held in a recovery tank until they regained equilibrium and were then released into the river above or below the diversion structure according to where they were initially captured. In 1999, we implanted 16 fish below the diversion structure and 9 fish above with radio transmitters. In 2000, we implanted 30 fish with radio transmitters (15 above the diversion structure and 15 below).

We tracked radio-tagged fish with a hand-held loop antenna and a scanning receiver (Advanced Telemetry Systems, Model R2000). Beginning one week after surgical implantation of transmitters, we located fish bimonthly between October 1999 and June 2000. Improvements in our tracking techniques during our second study year allowed us to track fish weekly between October 2000 and May 2001. We tracked fish on foot, ski, all-terrain vehicle, or boat, depending on seasonal conditions. On 11 occasions, we tracked from an airplane (Mountain Air Research, Driggs, Idaho) to locate fish that moved out of the study area. We plotted fish locations on an aerial photograph of the refuge property when applicable and recorded Universal Transverse Mercator coordinates with a handheld Global Positioning System unit. We later mapped these coordinates by means of geographical information systems (GIS) and digital stream coverages for southeastern Idaho and the central and upper Bear River watersheds. All distances between locations were calculated in the GIS and rounded to the nearest 50 m, except for distances involving locations from an airplane, which were rounded to the nearest 100 m.

Because of stream conditions and the inherent limitations of a telemetry study, we developed a set of rules with which to filter our initial data set before statistical analysis. Turbidity and water depth prevented visual contact with fish, and we were able to confirm that fish were alive only through subsequent displacements (i.e., when we located a fish at a different location on a later

TABLE 1.—Descriptive statistics for median home ranges (m) and frequencies of movement of radio-tagged Bonneville cutthroat trout between October and March of 1999–2000 and 2000–2001 in the Thomas Fork and Bear River, Idaho–Wyoming. Site refers to location relative to a diversion structure. Differences in sample size for the two movement metrics result from the fact that fish that were not located frequently enough to include in home range calculations were included in frequency-of-movement calculations. Movements per contact is the ratio of movements greater than 50 m to contacts.

Site	Year	Home range			Movements per contact				
		<i>N</i>	Median home range (range)	Mean number of relocations (range)	<i>N</i>	Mean	SD	Median	Range
Below	1999–2000	14	800 (250–11,200)	8 (2–11)	14	0.61	0.25	0.59	0.25–1.00
	2000–2001	13	600 (50–10,400)	12 (2–19)	13	0.45	0.33	0.41	0.00–1.00
Above	1999–2000	7	1,600 (150–21,500)	11 (10–11)	8	0.69	0.22	0.73	0.31–0.92
	2000–2001	14	3,700 (2,500–8,900)	15 (8–19)	15	0.89	0.11	0.90	0.57–1.00

tracking occasion, we assumed that the fish was alive on the previous occasion). As a result, we included in our data set only those locations for which another location in a different place was later obtained; for example, if a fish was found in the same location for several weeks leading up to the end of the study or to transmitter battery failure, then only the first location at that spot was included in the data set. In order for an individual's movements to be included in the range calculations for a given season, at least one location must have been obtained for that individual during the last month of that season.

We evaluated the degree of mobility in our study population using frequency of movements (movements per contact: Simpkins et al. 2000). We defined movement as a displacement of over 50 m between consecutive contacts of individual fish and nonmovement as any displacement less than 50 m. We assigned a value of one for dates on which a movement was observed and a value of zero for dates on which no movement was observed. We then obtained a metric of movements per observation for each fish. We were able to achieve a normal distribution through an arcsine transformation of these data, so we chose to use analysis of variance (ANOVA) rather than pairwise nonparametric comparisons (which would have required some form of correction for the multiple pairwise tests) to test for differences between years, between seasons, and influence of the diversion structure.

We computed home ranges by measuring the longitudinal distance from the most upstream location to the most downstream location (Young 1994). We grouped fish according to their location relative to the diversion (above versus below) and the year in which they were tracked (1999–2000 or 2000–2001). We delineated seasons as follows:

fall: September 1–November 30; winter: December 1–March 15; spring: March 16–May 31; and summer: June 1–August 31. Because of small sample sizes and nonnormal distributions, we used a three-way ANOVA on the ranked home ranges using year, season, and location (above or below the diversion) as factors. All analyses were performed with SAS (SAS Institute 1999), and relationships were considered significant at $P < 0.05$.

We deployed nine StowAway TidBiT temperature data loggers (Onset Computer Corporation, Pocasset, Massachusetts) at approximately 1-km intervals throughout our study site in the lower Thomas Fork and Bear River. We programmed these thermographs to record temperature in °C at 30-min intervals throughout the 2-year study period.

Results

On average our study fish moved greater distances and more frequently than we expected. Seven of the original 55 radio-tagged fish were not relocated consistently enough to be included in our analyses. We considered those fish that occupied home ranges of 1 km or greater during our study period to be mobile. Eleven of 21 fish (52%) moved at least 1 km between October 1999 and March of 2000, and 16 of 27 (59%) moved that distance over the same period during 2000–2001 (Table 1). During the winter months (December–February), 17% of fish ranged at least 1 km in 1999–2000 and 54% ranged at least 1 km in 2000–2001 (Table 2). Similarly, the average number of movements per contact indicated that fish frequently moved more than 50 m between contacts (Table 1), but we found no difference between years (ANOVA: $P > 0.0500$; $\bar{x} = 0.65$ in 1999–2000; $\bar{x} = 0.65$ in 2000–2001), between seasons (ANOVA: $P > 0.0500$; $\bar{x} = 0.66$ in fall; $\bar{x} = 0.64$

TABLE 2.—Descriptive statistics for median home ranges of radio-tagged Bonneville cutthroat trout in the Thomas Fork and Bear River, Idaho–Wyoming, by season and study year.

Year	Season	N	Median home range (m)	Range (m)	Number of mobile fish with home range > 1 km (%)
1999–2000	Fall	20	625	<50–3,900	7 (35%)
	Winter	18	300	100–18,500	3 (17%)
2000–2001	Fall	25	2,100	<50–4,150	14 (56%)
	Winter	26	1,900	<50–10,400	14 (54%)

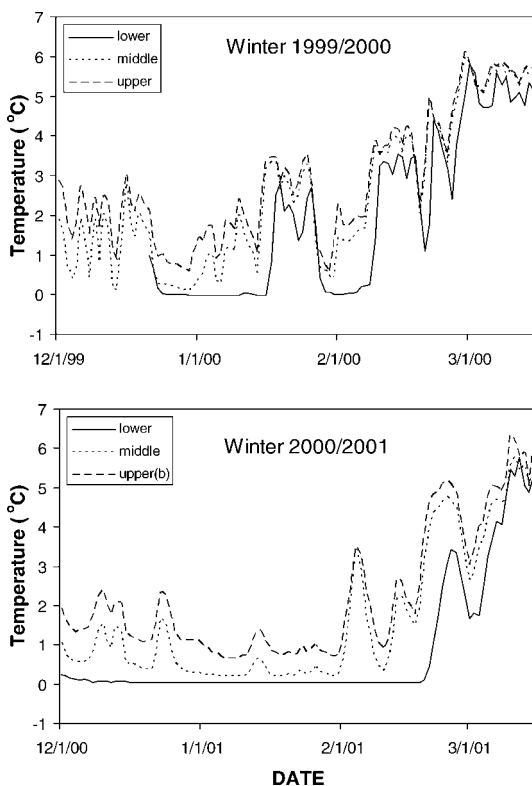


FIGURE 2.—Mean daily stream temperatures at three thermograph sites in the Thomas Fork and Bear River, Idaho–Wyoming, from December 1, 1999, to March 15, 2000, and from December 1, 2000, to March 15, 2001. The upper thermograph was located in the Thomas Fork at the upstream end of our study site. The middle thermograph was located in the Thomas Fork 4 km downstream from the upper site. The lower thermograph was located at the confluence of the Thomas Fork and Bear River, 7 km downstream from the upper site. The upper thermograph was lost after the first year of the study. As a result, the upper thermograph for the plot of winter 2000–2001 was located 1 km downstream from the upper thermograph in the plot of winter 1999–2000.

in winter), or the interaction of year and season when considering the population as a whole. However, further analysis of movements per contact showed that fish above the diversion moved significantly more often than fish below the diversion during 2000–2001 (ANOVA: $P < 0.0001$; Table 1).

We found considerable variation in the movements and home ranges of BCT on weekly, seasonal, and annual bases. Fish occupied larger seasonal home ranges during the second study year than during the first (ANOVA: $P = 0.0007$; median = 1,600 m in 1999–2000; median = 5,375 m in 2000–2001). However, annual home ranges during both years were skewed by extensive spring migrations, and we were unable to detect significant differences between years when we pooled seasonal home ranges into annual home ranges (ANOVA: $P = 0.1500$; median). Similarly, we found no statistically significant differences in home ranges among seasons (ANOVA: $P = 0.1800$; median = 800 m in fall; median = 675 m in winter; median = 1,025 m in spring) because of the wide variation of movement behaviors within each season. Most of our fish moved what we consider to be large distances (i.e., >1 km) at some point in our study, and many were highly mobile throughout the study.

We found that home ranges during our study were significantly larger for fish above the diversion than for those below (ANOVA: $P = 0.0003$; median = 2,225 m above; median = 500 m below). In all but one instance, BCT that were tagged upstream from the diversion structure remained above the diversion throughout the tracking period. In both years, fish tagged below the structure occupied home ranges in the Thomas Fork and Bear River, and several fish regularly moved between the two. All fish that were tagged downstream from the diversion structure remained below the diversion, although many fish were observed attempting to ascend the structure during

the first week of May 2001. None of these observed fish were radio-tagged, so we cannot empirically prove or disprove that the structure was a complete barrier; however, based on our observations, we believe that upstream passage was not possible between May and September of that year. We observed BCT at the structure for approximately 2 h, during which time we witnessed repeated attempts to leap the structure. The splash pad at the base of the spillway precluded any deep-water starting zone, and fish were, therefore, forced to initiate their leaps from over 2 m away from the structure. Given this approach distance, we believe that it would be impossible for them to leap over the 1.5-m spillway.

During the 2 years of this study, several fish made what we consider to be extensive spawning migrations (i.e., >30 km; Figure 1). Although our sample size of these fish was too small for statistical analysis, a description of movements is informative. One female was killed by an angler in Salt Creek on May 20, 2000 (59 km upstream from the study site) 224 d after it was tagged in 1999. The angler described this fish as being full of eggs, and it was captured in a tributary believed to be used by fluvial Bear River BCT for spawning. During the second year of the study, we tracked 4 fish that moved downstream out of Thomas Fork beginning in April. These fish then moved 33 km upstream in the Bear River to its confluence with Smith's Fork. One fish remained at the confluence and was not confirmed alive after this point, while the other three moved up the Smith's Fork 7, 14, and 53 km, respectively. Two other fish tracked throughout the winter and into the spring disappeared between April 12 and May 25, but were later relocated in the Bear River after the end of the spawning season.

Thermograph data from three sites show a trend toward warmer mean daily temperatures at upstream locations during both study years, and average water temperatures were slightly warmer during the winter of 1999–2000 than during 2000–2001 (Figure 2).

Discussion

Fluvial BCT in this study were more mobile than we expected during fall and winter. Home ranges before spring (i.e., October–March) ranged from less than 50 m to 10,400 m (median = 2,800 m) in 2000–2001 and from 150 m to 21,500 m (median = 900 m) in 1999–2000. Home ranges were significantly larger during the second year of our study, and we suspect that this difference may be

attributable to a greater range of water temperatures among sites (Figure 2) and lower streamflows (personal observation) during 2000–2001. However, during both study years, radio-tagged fish moved frequently and occupied larger home ranges than we expected, especially during the winter months. Whereas large-scale seasonal migrations have been documented in a few cutthroat trout populations that still inhabit large river systems (Bjornn and Mallet 1964; Clancy 1988; Schmetterling 2001, 2003), most studies have shown winter home ranges to be limited. For example, Schmetterling (2001) found that fluvial westslope cutthroat trout in Montana did not move more than 100 m during overwintering, and Hilderbrand and Kershner (2000b) found that only 3 of 9 radio-tagged BCT in a small headwater population moved between December and April. The largest observed winter movement in that study was 188 m. In separate studies of westslope cutthroat trout in Montana and Alberta, investigators found that these fish overwintered in short reaches of river (i.e., <200 m), except during anchor ice formation when they were forced to move to more suitable habitats (Jakober et al. 1998; Brown 1999). In contrast, we observed winter movements that were extensive and frequent. Winter home ranges (i.e., December–February) of BCT in our study ranged from less than 50 m to 10,350 m across sites and years, mobile individuals accounted for 17% and 54% of study populations during our 2-year study, and several individuals exhibited substantial movements (up to 18.5 km) during winter months (Table 2).

Most salmonid research has documented that stream-dwelling populations comprise a large sedentary component and a smaller mobile one. Rodriguez (2002) looked at studies of 27 salmonid populations, including brook (*Salvelinus fontinalis*), brown, cutthroat, and rainbow trout, and found that the median proportion of mobile individuals within these study populations was 19%. Similarly, Hilderbrand and Kershner (2000b) found that 61% of individuals in a headwater population of BCT were recaptured less than 300 m away from their initial release point after 1 year. In contrast, mobile fish in our study (i.e., home range > 1 km) accounted for 52% and 59% of our populations between October and April of the 2 years, respectively, and fish were found at least 50 m away from their previous locations roughly 66% of the time (Table 1). Whereas we acknowledge that the movements-per-contact metric may introduce bias by creating larger estimates for fish that are con-

tacted less often, our data did not appear to be skewed in that direction; in fact, it appeared that fish that we contacted more often had larger estimates of movements per contact. We believe that this metric helps to illustrate the relative mobility of our study fish when compared with previous studies in which researchers have most often used a median displacement value of 50 m as the upper limit to delineate between mobile and sedentary populations (Rodriguez 2002, and references therein), and most have concluded that the majority of individuals within salmonid populations exhibit restricted movement.

There are multiple explanations for the extensive winter home ranges and large mobile population component that we observed. Winter movements in the Thomas Fork and Bear River could be driven by water temperatures and the dual constraints of piscivory and winter metabolic requirements. Stream salmonids have been shown to continue feeding throughout the winter (Chapman and Bjornn 1969; Cunjak et al. 1987; Hebdon and Hubert 2001), and BCT even maintain growth during the winter in some systems (Trotter 1987; Behnke 1992; Ruzycki et al. 2001). Like brown trout (Clapp et al. 1990; Young 1994), BCT probably shift to piscivory as they attain large sizes (Nielson and Lentsch 1988; Behnke 1992; Ruzycki et al. 2001). Some research suggests that a shift to piscivory may require fish to forage more widely than does drift feeding on invertebrates (Clapp et al. 1990; Young 1994, and references therein). Although we did not specifically test this hypothesis during our study, the idea that BCT in the Bear River are piscivorous is supported by our finding juvenile carp (*Cyprinus carpio*) in the stomachs of Thomas Fork BCT captured in early fall (Colyer 2002). We speculate that winter water temperatures (2–4°C; Figure 2) in the Thomas Fork probably allow BCT to continue foraging and, therefore, may explain the unexpected ranging behavior that we observed. Alternatively, the extensive movements we observed might be a function of habitat homogeneity at our study site. Adult trout tend to seek out deep water with low-flow velocities during winter (Cunjak and Power 1986; Chisholm and Hubert 1987; Brown and Mackay 1995; Jakober et al. 1998; Brown 1999; Muhlfeld et al. 2001) and may avoid shallow, faster-moving water (Brown and Mackay 1995) typically associated with riffles (see discussion of summer riffle–pool movements in Lonzarich et al. 2000). The Thomas Fork and Bear River are low-gradient systems and neither has many riffle sequences. Instead, these

streams comprise only runs and pools, and fish can move long distances without encountering shallow habitats.

We found evidence of life history interruption due to the observed impacts of the diversion barrier on our study population. Our hypothesis that the diversion structure influences fish movements was supported by the apparent inability of fluvial BCT to ascend the structure during upstream spawning migrations and by the differences in movements between fish above and below the barrier. During the first year of our study, the diversion structure allowed for fish passage during the winter and early spring. During the second year, however, the diversion remained closed to fish passage throughout the year. In May of that year, we documented repeated unsuccessful attempts at passage by staging BCT (our unpublished data). Our subsequent belief that all fluvial spawning migrations into the Thomas Fork were prevented during that year was supported by information gathered during a concurrent telemetry study in upstream tributaries to the Thomas Fork (Schrack 2002). In that study, large fluvial BCT in upstream spawning tributaries had been captured and implanted with radio transmitters in each of the previous two springs. During 2001, while the diversion structure on the lower Thomas Fork remained closed, researchers found no fluvial spawners in upstream tributaries (Schrack 2002).

Regardless of fish position relative to the diversion barrier, five fish made extensive spawning migrations, traveling 33, 37, 44, 59, and 86 km. One of these fish occupied a home range above the diversion structure from October 1999 to April 2000 before moving into an upstream tributary to the Thomas Fork in May 2000. The other four fish occupied home ranges below the diversion structure until spring 2001, when they traveled downstream out of Thomas Fork and into Bear River and eventually 33 km upstream and into Smith's Fork. These observations provide the first documentation of a fluvial connection between tributary-resident BCT populations in the upper Thomas and Smith's forks and main-stem fluvial populations in the Bear River. Fluvial BCT in this system appear to overwinter in lower-elevation main-stem reaches of the Thomas Fork, Smith's Fork, and Bear River, migrate upstream to spawn in tributary systems in the Thomas Fork and Smith's Fork, and return to the main stems in the fall. Whereas this type of large-scale seasonal migration between spawning tributaries and main-stem habitats more suitable for overwintering is common in some sal-

monid populations (Cunjak and Power 1986; Chisholm and Hubert 1987; Meyers et al. 1992; Jakober et al. 1998), it has seldom been documented for interior cutthroat trout (but see Bjornn and Mallet 1964; Schmetterling 2001, 2003).

Implications

The extensive home ranges, large-scale seasonal migrations, and important mobile component within our study population suggest that effective conservation of fluvial BCT will require management at much larger spatial scales than are typically considered for interior cutthroat trout. The "conservation by isolation" method historically favored by managers has typically focused restoration and protection efforts on short stream reaches (<10 km; Harig and Fausch 2002) in high-elevation tributaries. Our data suggest that this approach will not accommodate the large range of movement behaviors exhibited by BCT populations within the Bear River. The differences in home ranges between fish above and below the diversion structure and the apparent inability of fish to get past the structure in some years suggest that seasonal movement barriers affect behaviors within populations and can alter fish distributions throughout a watershed. Further, our results suggest that fluvial BCT in the Thomas Fork and Bear River use different sections of stream during different seasons, and that population data collected during typical field seasons (June–September) probably misrepresent actual distributions and abundances throughout much of the year.

The fluvial connection between tributary populations in Thomas and Smith's forks and main-stem habitats in the Bear River suggests that conservation approaches that focus exclusively on headwater systems are incomplete. Habitat improvements, land use mitigation, and special harvest regulations in Bear River tributary headwaters have been implemented to protect spawning areas and resident BCT populations on federal land. To date, habitat conditions and population trends within the privately owned main-stem reaches of the lower Thomas Fork, lower Smith's Fork, and Bear River will be required to ensure the long-term persistence of fluvial BCT in this system.

Acknowledgments

We thank the U.S. Fish and Wildlife Service and the Fish and Aquatic Ecology Unit of the U.S.

Forest Service for funding this project. The Ecology Center at Utah State University provided financial support in the form of a research grant and travel compensation. Todd Crawl, James Dobrowski, Michael Young, and David Schmetterling provided insightful comments on earlier drafts of this manuscript. This is University of Maryland, Center for Environmental Science, Appalachian Laboratory Scientific Series 3820.

References

- Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society, Monograph 6, Bethesda, Maryland.
- Bernard, D. R., and E. K. Israelsen. 1982. Inter- and intrastream migration of cutthroat trout (*Salmo clarki*) in Spawn Creek, a tributary of the Logan River, Utah. *Northwest Science* 56:148–158.
- Bidgood, G. F. 1980. Field surgical procedure for implantation of radio tags in fish. Alberta Fish and Wildlife Division, Fisheries Research Report 20, Edmonton.
- Bjornn, T. C., and J. Mallet. 1964. Movements of planted and wild trout in an Idaho river system. *Transactions of the American Fisheries Society* 93:70–76.
- Brown, R. S. 1999. Fall and early winter movements of cutthroat trout (*Oncorhynchus clarki*), in relation to water temperature and ice conditions in Dutch Creek, Alberta. *Environmental Biology of Fishes* 55:359–368.
- Brown, R. S., and W. C. Mackay. 1995. Fall and winter movements of and habitat use by cutthroat trout in the Ram River, Alberta. *Transactions of the American Fisheries Society* 124:873–885.
- Chapman, D. W., and T. C. Bjornn. 1969. Distribution of salmonids in streams, with special reference to food and feeding. Pages 153–176 in T. G. Northcote, editor. *Symposium on salmon and trout in streams*. Institute of Fisheries, University of British Columbia, Vancouver.
- Chisholm, I. M., and W. A. Hubert. 1987. Winter stream conditions and use of habitat by brook trout in high-elevation Wyoming streams. *Transactions of the American Fisheries Society* 116:176–184.
- Clancy, C. G. 1988. Effects of dewatering on spawning by Yellowstone cutthroat trout in tributaries to the Yellowstone River, Montana. Pages 37–41 in R. E. Gresswell, editor. *Status and management of interior stocks of cutthroat trout*. American Fisheries Society, Symposium 4, Bethesda, Maryland.
- Clapp, D. F., R. D. Clark, and J. S. Diana. 1990. Range, activity, and habitat of large, free-ranging brown trout in a Michigan stream. *Transactions of the American Fisheries Society* 119:1022–1034.
- Colyer, W. T. 2002. Seasonal movements of fluvial Bonneville cutthroat trout in the Thomas Fork of the Bear River, Idaho–Wyoming. Master's thesis. Utah State University, Logan.
- Cunjak, R. A., R. A. Allen, and G. Power. 1987. Sea-

- sonal energy budget of brook trout in streams: implications of a possible deficit in early winter. *Transactions of the American Fisheries Society* 116:817–828.
- Cunjak, R. A., and G. Power. 1986. Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences* 43:1970–1981.
- Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65:169–175.
- Gilpin, M. E., and M. E. Soule. 1986. Minimum viable populations: processes of species extinction. Pages 13–34 in M. E. Soule, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts.
- Gresswell, R. E. 1988. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, Maryland.
- Harig, A. L., and K. D. Fausch. 2002. Minimum habitat requirements for establishing translocated cutthroat trout populations. *Ecological Applications* 12:535–551.
- Hebdon, J. L., and W. A. Hubert. 2001. Body conditions and stomach contents of subadult trout during fall and winter in three Wyoming tailwaters. *North American Journal of Fisheries Management* 21:897–903.
- Henderson, R. H. 1999. Spawning strategies and hybridization potential of cutthroat, rainbow, and hybrid trout in a large river. Master's thesis. Utah State University, Logan.
- Henderson, R., J. L. Kershner, and C. A. Toline. 2000. Timing and location of spawning by nonnative wild rainbow trout and native cutthroat trout in the South Fork Snake River, Idaho, with implications for hybridization. *North American Journal of Fisheries Management* 20:584–596.
- Hilderbrand, R. H. 2003. The roles of carrying capacity, immigration, and population synchrony on persistence of stream-resident cutthroat trout. *Biological Conservation* 110:257–266.
- Hilderbrand, R. H., and J. L. Kershner. 2000a. Conserving inland cutthroat trout in small streams: how much stream is enough? *North American Journal of Fisheries Management* 20:513–520.
- Hilderbrand, R. H., and J. L. Kershner. 2000b. Movement patterns of stream-resident cutthroat trout in Beaver Creek, Idaho–Utah. *Transactions of the American Fisheries Society* 129:1160–1170.
- Jakober, M. J., T. E. McMahon, R. F. Thurow, and C. G. Clancy. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. *Transactions of the American Fisheries Society* 127:223–235.
- Johnstone, H. C., and F. J. Rahel. 2003. Assessing temperature tolerance of Bonneville cutthroat trout based on constant and cycling temperature regimes. *Transactions of the American Fisheries Society* 132:92–99.
- Kershner, J. L. 1995. Bonneville cutthroat trout. Pages 28–35 in M. K. Young, editor. *Conservation assessment for inland cutthroat trout*. U.S. Forest Service, General Technical Report RM-256, Fort Collins, Colorado.
- Liknes, G. A., and P. J. Graham. 1988. Westslope cutthroat trout in Montana: life history, status, and management. Pages 53–60 in R. E. Gresswell, editor. *Status and management of interior stocks of cutthroat trout*. American Fisheries Society, Symposium 4, Bethesda, Maryland.
- Lonzarich, D. G., M. R. Lonzarich, and M. L. Warren, Jr. 2000. Effects of riffle length on the short-term movement of fishes among stream pools. *Canadian Journal of Fisheries and Aquatic Sciences* 57:1508–1514.
- Martin, M. A., and D. K. Shiozawa. 1982. The electrophoresis of isolated trout populations from selected Utah streams. Report to the Utah Division of Wildlife Resources, Salt Lake City.
- Meyers, L. S., T. F. Thuemler, and G. W. Kornely. 1992. Seasonal movements of brown trout in northeast Wisconsin. *North American Journal of Fisheries Management* 12:433–441.
- Morita, K., and S. Yamamoto. 2002. Effects of habitat fragmentation by damming on the persistence of stream-dwelling charr populations. *Conservation Biology* 16:1318–1323.
- Morita, K., S. Yamamoto, and N. Hoshiro. 2000. Extreme life history change of white-spotted char (*Salvelinus leucomaenis*) after damming. *Canadian Journal of Fisheries and Aquatic Sciences* 57:1300–1306.
- Moyle, P. B., and G. M. Sato. 1991. On the design of preserves to protect native fishes. Pages 155–170 in W. L. Minckley and J. E. Deacon, editors. *Battle against extinction: native fish management in the American West*. University of Arizona Press, Tucson.
- Muhlfeld, C. C., D. H. Bennett, and B. Marotz. 2001. Fall and winter habitat use and movement by Columbia River redband trout in a small stream in Montana. *North American Journal of Fisheries Management* 21:170–177.
- Nielson, B. R., and L. Lentsch. 1988. Bonneville cutthroat trout in Bear Lake: status and management. Pages 128–133 in R. E. Gresswell, editor. *Status and management of interior stocks of cutthroat trout*. American Fisheries Society, Symposium 4, Bethesda, Maryland.
- Northcote, T. G. 1992. Migration and residency in stream salmonids: some ecological considerations and evolutionary consequences. *Nordic Journal of Freshwater Research* 67:5–17.
- Northcote, T. G., S. N. Willisroft, and H. Tsuyuki. 1970. Meristic and lactate dehydrogenase genotype differences in stream populations of rainbow trout below and above a waterfall. *Journal of the Fisheries Research Board of Canada* 27:1987–1995.
- Novinger, D. C., and F. J. Rahel. 2003. Isolation management with artificial barriers as a conservation

- strategy for cutthroat trout in headwater streams. *Conservation Biology* 17:772–781.
- Rieman, B. E., and F. W. Allendorf. 2001. Effective population size and genetic conservation criteria for bull trout. *North American Journal of Fisheries Management* 21:756–764.
- Rieman, B. E., and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. U.S. Forest Service, General Technical Report INT-302, Ogden, Utah.
- Rieman, B. E., and J. D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. *Transactions of the American Fisheries Society* 124:285–296.
- Rodriguez, M. A. 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. *Ecology* 83:1–13.
- Ruzycki, J. R., W. A. Wurtsbaugh, and C. Luecke. 2001. Salmonine consumption and competition for endemic prey fishes in Bear Lake, Utah–Idaho. *Transactions of the American Fisheries Society* 130:1175–1189.
- SAS Institute. 1999. SAS OnlineDoc, version 8. SAS Institute, Cary, North Carolina.
- Schill, D. J., R. Thurow, and P. K. Kline. 1994. Seasonal movement and spawning mortality of fluvial bull trout in Rapid River, Idaho. Idaho Department of Fish and Game, Federal Aid in Sport Fish Restoration, Job Performance Report, Project F-73-R-15, Boise.
- Schmetterling, D. A. 2001. Seasonal movements of fluvial westslope cutthroat trout in the Blackfoot river drainage, Montana. *North American Journal of Fisheries Management* 21:507–520.
- Schmetterling, D. A. 2003. Reconnecting a fragmented river: movements of westslope cutthroat trout and bull trout after transport over Milltown Dam. *North American Journal of Fisheries Management* 23:721–731.
- Schrank, A. J. 2002. Ecological significance of movement patterns of Bonneville cutthroat trout in a western Wyoming watershed. Doctoral dissertation. University of Wyoming, Laramie.
- Schrank, A. J., F. J. Rahel, and H. C. Johnstone. 2003. Evaluating laboratory-derived thermal criteria in the field: an example involving Bonneville cutthroat trout. *Transactions of the American Fisheries Society* 132:100–109.
- Shiozawa, D. K., and R. P. Evans. 1995. The genetic status of cutthroat trout from various drainages in the Wasatch-Cache National Forest based on examination of mitochondrial DNA. Interim Report to the U.S. Forest Service, Contract 43-8490-4-0110, Salt Lake City, Utah.
- Simpkins, D. G., W. A. Hubert, and T. A. Wesche. 2000. Effects of fall-to-winter changes in habitat and frazil ice on the movements and habitat use of juvenile rainbow trout in a Wyoming tailwater. *Transactions of the American Fisheries Society* 129:101–118.
- Stacey, P. B., and M. Taper. 1992. Environmental variation and the persistence of small populations. *Ecological Applications* 2(1):18–29.
- Stuber, R. J., B. D. Rosenlund, and J. R. Bennett. 1988. Greenback cutthroat trout recovery program: management overview. American Fisheries Society, Pages 71–74 in R. E. Gresswell, editor. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, Maryland.
- Swanberg, T. R. 1997. Movements of and habitat use by fluvial bull trout in the Blackfoot River, Montana. *Transactions of the American Fisheries Society* 126:765–746.
- Thurow, R. F., C. E. Corsi, and V. K. Moore. 1988. Status, ecology, and management of Yellowstone cutthroat trout in the upper Snake River drainage, Idaho. Pages 25–36 in R. E. Gresswell, editor. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, Maryland.
- Trotter, P. C. 1987. Cutthroat: native trout of the West. Colorado Associated University Press, Boulder.
- West, R. L. 1992. Autumn migration and overwintering of arctic grayling in coastal streams of the Arctic National Wildlife Refuge, Alaska. *Transactions of the American Fisheries Society* 121:709–715.
- Winter, J. 1996. Advances in underwater biotelemetry. Pages 555–590 in B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Young, M. K. 1994. Mobility of brown trout in south-central Wyoming streams. *Canadian Journal of Zoology* 72:2078–2083.
- Young, M. K. 1995. Conservation assessment for inland cutthroat trout. U.S. Forest Service, General Technical Report RM-GTR-256, Fort Collins, Colorado.
- Young, M. K. 1996. Summer movements and habitat use by Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) in small, montane streams. *Canadian Journal of Fisheries and Aquatic Sciences* 53:1403–1408.
- Young, M. K., and A. L. Harig. 2001. A critique of the recovery of greenback cutthroat. *Conservation Biology* 15:1575–1584.